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NEW WINES IN A NEW BOTTLE

IN ANSWER TO many encouraging requests, especially that our Bulletin be better bound, we have adopted the format now in your hands. We hope it works and that you like it.

AT THE EIGHTH Stated Meeting of the NRP in mid-August, several Associates reported on the NRP-related research being conducted at their laboratories. A brief rundown of such research is included in the report of the meeting, which begins on page 33.

ONE SUCH ASSOCIATE was Melvin Calvin, who summarized the unsuccessful attempts of his laboratory to confirm the published claims that planarian flatworms are trainable. As soon as Professor Calvin finished speaking on this controversial subject, we asked him to send us a discussion paper based on his talk. The resulting paper, co-authored by Dr. Edward Bennett, begins on page 3.

IF PLANARIANS CANNOT be reliably trained, interest should logically shift to other species higher up the evolutionary scale. A pithy discussion paper in this issue suggests three such species, in an argument about an experiment that could settle the question of whether nervous systems store information as processes, or changes in structure. The paper, by Dr. Harold J. Morowitz of Yale, begins on page 25.

THE IN-HOUSE firing power of the NRP Center has been increased by the welcome arrival here of our latest Resident, Mr. Charles M. Fair; a science librarian, Mr. George Adelman; and a science writer-editor, J. Carolyn Register, M.D. Mr. Fair is the author of The Physical Foundations of the Psyche (Wesleyan, 1963), for which he received a John Simon Guggenheim Memorial Fellowship last year -- spent in the laboratory of Donald B. Lindsley at the Brain Research Institute of UCLA. Mr. Adelman comes to us from ONR, and Dr. Register from the University of Rochester Medical Center and, previously, the Rogosin Laboratories directed by Dr. Albert L. Rubin at Cornell Medical Center. The incumbent Communications Staff greets all three newcomers and looks forward to their help in further improving the NRP Bulletin. --T.M.

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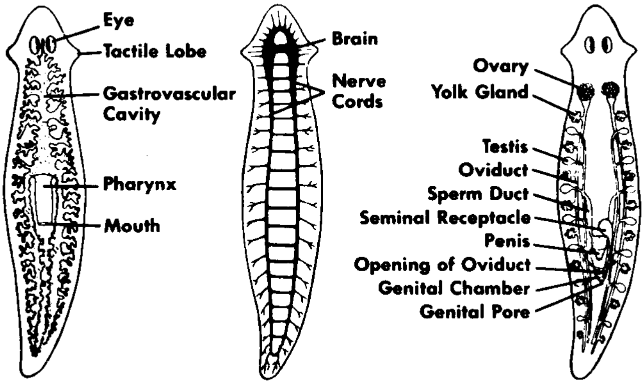
Frontispiece: PLANARIAN MORPHOLOGY



The Planaria flatworm lives in fresh water and is about ½-in. long. Its mouth, located in the middle of its under surface, leads to a blind digestive cavity (left). Its simple nervous system (center) is of the so-called ladder type. The tactile lobes are sensitive to touch, and possibly to other stimuli. The reproductive system (right) features organs of both sexes in a single individual. (After Kenoyer)[Reproduced from page 1265 of The Harper Encyclopedia of Science, ed. by James R. Newman (Harper & Row, 1963).]

FAILURE TO TRAIN PLANARIANS RELIABLY

A Discussion Paper Summarizing
Experiments Performed During
1962-1964

by

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CONTENTS

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PREFACE

The importance of a simple biological system with which to investigate possible biochemical bases for learning is manifest. Many scientists, as well as the lay public, have been excited by recent reports of learning in planarians[1] and by experiments indicating that this learning can be transmitted by means normally considered unconventional, i.e. during regeneration or by cannibalism.[2] These experiments have suggested that, during learning, intracellular biochemical changes occur which may be investigated by modern scientific methods.

Prior to commencing investigations of biochemical correlates of learning in planarians, it is necessary to have reliable means to train planarians and to quantify this training. The methods used to demonstrate learning in planarians have been thoroughly reviewed by Jacobson.[1] In addition numerous informal reports of training and its transfer have appeared.[3] With the exception of the studies by McConnell and co-workers, the reports of training of planarians have been characterized by a lack of further reports by the same or other investigators in which the experiments have been replicated or extended.

The following is a summary of our unrewarded efforts, over a 2 year period, to train planarians. Although it would be presumptuous to conclude that planarians cannot be trained, we do conclude that at the present time, the relevant factors necessary for reproducible and reliable training of planarians have not been described with sufficient precision to permit their use in studies of the biochemical bases of learning. The importance of the control of subtle factors in the care and training of planarians has recently been emphasized by McConnell[4] and by Brown and Beck.[5]

RESULTS OF TRAINING EXPERIMENTS

The methods by which we have attempted to train planarians fall into five main categories: classical conditioning, light habituation, maze training, operant conditioning, and food reward. All of our training methods have been patterned, usually as closely as possible, after previously described methods. In this report, only a brief description of methods and results is included; a fuller account will be available.[6]

I. (A) Classical Conditioning

Classical conditioning of planarians was first described by Thompson and McConnell.[7] The subject is administered paired stimuli, the second of which is "punishing". Typically the training procedure has consisted of 3 seconds of light paired with shock during the last second. With planarians, the positive or "learned" response has been variously described as stopping, turning, or "scrunching" during the light stimulus, before the onset of the shock. Planarians trained by classical conditioning have been reported to retain this learning upon bisection and regeneration of either head or tail portion.[2] Conditioning has also been transmitted by cannibalism.[2]

In our laboratories, nine experiments with various conditions of voltage, number of trials per day, intensity of back-lighting, feeding regimes, sources of planarians, etc. were carried out during 1962-1963, using a total of about 60 planarians. The experimental apparatus was similar to that described by McConnell, Cornwell, and Clay.[8] The times of unconditioned stimulus (UCS) and conditioned stimulus (CS) were electronically controlled. In one experiment (Table 1), an increase in the average response rate from 20% to 60% of the total number of trials was observed, but this was significantly less than the preset criterion of 92%. The scores for individual planarians did not show a reliable and consistent pattern of improvement with trial sets. In another experiment the criterion was lowered to 18 responses prior to shock on any 20 trials, including trials on two consecutive days. Training was discontinued at this point. Nine of the 14 subjects reached this lower criterion within 300 trials (Table 2).

Table 1: No. of responses to light by individual subjects (D. tigrina) per set of 25 classical conditioning training trials. Subject: D.tigrina from Ann Arbor, Michigan (a source that had previously yielded good conditioners). CS: Two 100-watt bulbs delivering 3-second flashes. UCS: Output of 6-volt dry cell passed through a Harvard Apparatus Co. inductorium. Back-light: 7-1/2 watt bulb. No. of trials per day: 25.

	Worm Number										
Trial Sets	1	2	3	4	5	6	7	8	9	10	Average
1	6	3	6	2	3	6	3	7	5	5	4.6
2	8	4	7	7	5	10	9	6	8	11	7.5
3	7	12	6	6	6	12	13	9	13	6	9.0
4	7	9	6	4	3	16	8	10	7	3	7.3
5	9	7	10	5	14	15	14	9	8	3	9.4
6	8	10	12	3	7	11	11	16	6	8	9.2
7	6	8	7	10	12	15	11	12	16	7	10.4
8	11	10	8	8	11	10	11	13	15	14	11.1
9	15	11	10	19	5	8	13	16	17	17	13.1
10	10	14	12	19	17	16	9	15	8	15	13.5
11	12	10	15	20	5	4	14	11	12	8	11.1
12	6	14	12	19	3	12	13	17	9	6	11.1
13	14	15	16	20	7	12	17	20	15	14	15.0
14	10	9	14	21	16	14					14.0
15	15	8	15	19	10	15					13.7
16	19	10		11	12	8					12.0
17	15	18		11	15	11					14.0
18	20	19		17	15	13					16.8
19	12	11		13	17	20					14.6
20	18	12		15	13	15					14.6

Table 2: Number of responses to light by individual subjects (D. tigrina) per set of 20 training trials of classical conditioning*

Worm No.	Trial Sets 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	1	5	6	7	11	7	16	11	6	17**					
2	3	7	5	10	9	10	18**								
3	6	7	8	12	7	14	9**								
4	3	2	6	7	7	13	15	9	15	17**					
5	0	7	5	4	10	7	8	14	14	11	15	6	9	11	**18
6	0	5	4	3	11	11	14	10	15	15	13	11	8	16	14
7	2	7	5	6	11	9	12	13	15	15	16	16	10	13	15
8	1	7	7	13	6	10	14	13	9	14	14	11	13	10	14
9	3	8	11	12	8	17	14	18**							
10	1	1	1	2	5	13	7	4	6	7	9	11	7	8	8
11	4	4	6	3	5	13	9	14	5	11					
12	0	4	8	8	6	10	11	8	20**						
13	1	2	13	9	13	16	15	11**							
14	5	8	15	14	11	11	17	15	10**						
Av.	1.9	4.9	6.5	7.4	8.1	11.5	12.7								

* Subject: D. tigrina from Ann Arbor, Michigan.
CS, UCS, and back light were the same as in Experiment 4; number of trials per day was reduced to 20.

** Training was terminated when a subject responded at least 18 times during any 20 consecutive trials, which may have been held on two consecutive days.

No naive planarians were added during any training session of these two experiments. Therefore, there was no control for the possible effect of observer bias. In the remaining experiments, even less evidence of training was obtained.

(B) Classical Conditioning with Polarized Shock

Barnes and Katzung have reported that polarized cathodal shock (head oriented towards cathode) with a square wave from a Grass stimulator was even more effective as the UCS than shock obtained from an inductorium.(9) An increase in average response rate from 10% to greater than 80% was achieved with five days of training (25 trials/day). The high rate of response was retained through at least four subsequent days of testing using *D. tigrina* (Fig. 1). No data have been published on the retention or transfer of classical conditioning by this method.

We carried out 11 experiments using the procedure described by Barnes and Katzung. The principal obvious difference between our procedure and theirs was the inclusion of coded trainee and naive planarians in the design of some of these experiments, (Fig. 2). About 110 experimental planarians and 135 naive planarians from 3 different sources and 2 species were used. In one experiment (Fig. 4A and 4B) two experimenters tested 24 (twelve each) *D. dorotocephala* daily with cathodal shock. Of these, 12 were experimental subjects and 12 were "naives" replaced after each session. All worms were recoded daily. The average response rate found on the first day of testing was much higher than that reported by Barnes and Katzung. The marked daily variation in the response of an individual planarian is evident; thus, planarians No. 4 and No. 5 (Fig. 4A) gave a high initial response on the first day of testing which subsequently decreased during the next two or three days of testing. The response rate of planarian No. 3 did not increase until after seven days of training. On day 5, the response of five subjects tested by one of the trainers (CB) was high compared to the controls, but on day 6, only three subjects of this group had response rates above 80%, and on subsequent testing, no difference was apparent between the responses of experimental and naive subjects, (Fig. 3). The other trainer (Fig. 4B) was unable to distinguish the responses of experimental from naive planarians.

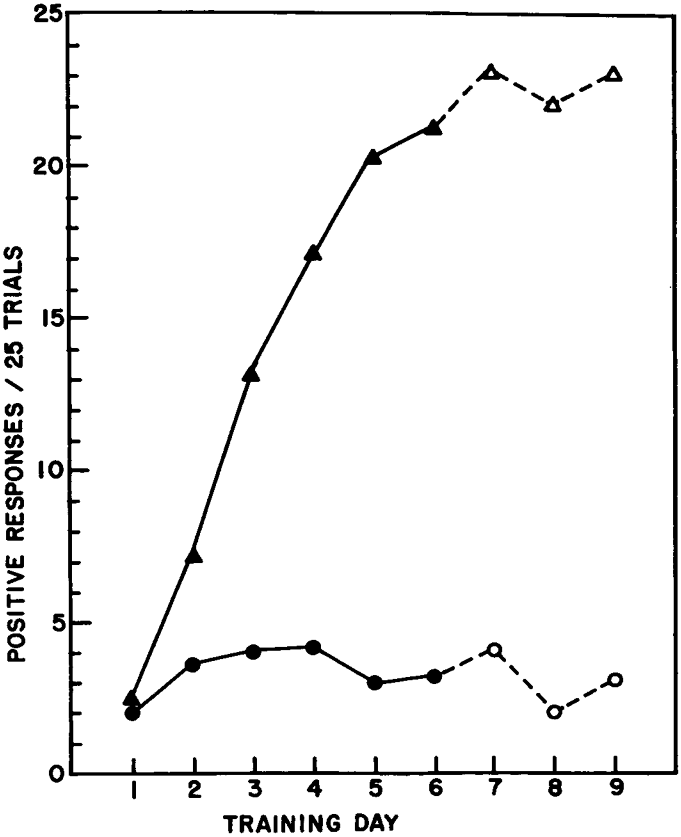
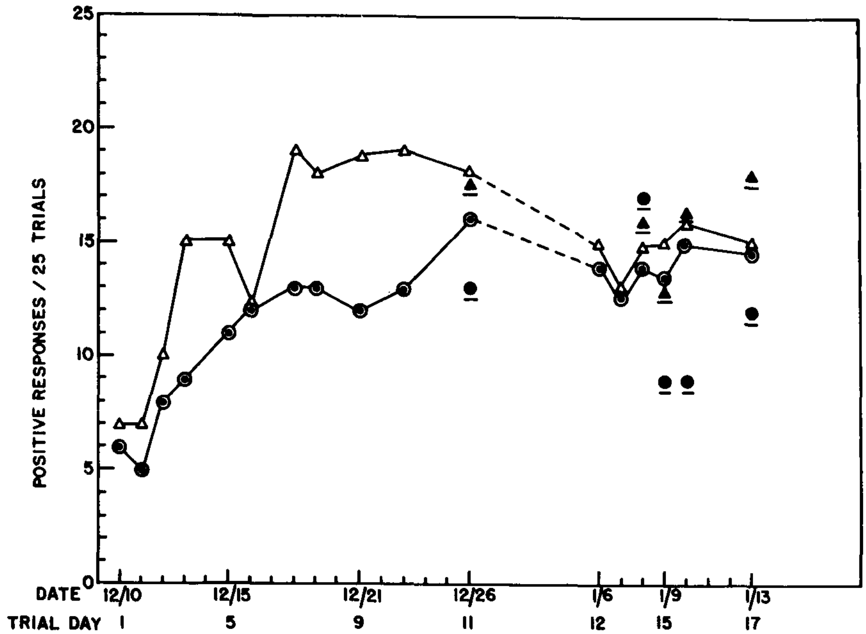


Figure 1. Responses (stops, turns, and contractions)/25 trials reported by Barnes and Katzung. Average of 15 planarians receiving tail shock (head towards cathode) ▲ ; average of 5 planarians receiving additional tail shock training △ ; average of 10 planarians receiving head shock (head towards anode) ● ; average of 5 planarians receiving additional head shock training ○ .



-Figure 2. Response/25 trials of 4 D. dorotocephala receiving tail shock (head towards cathode) △ and 4 planarians receiving head shock (tail towards cathode) ⊙ . The response of individual naive planarians tested during the later training days are indicated by the underlined ▲ (tail shock) and ● (head shock).

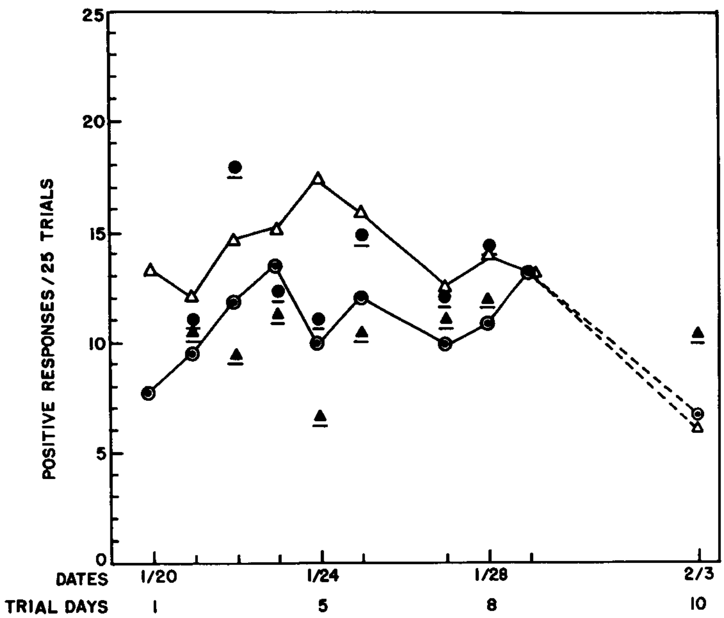
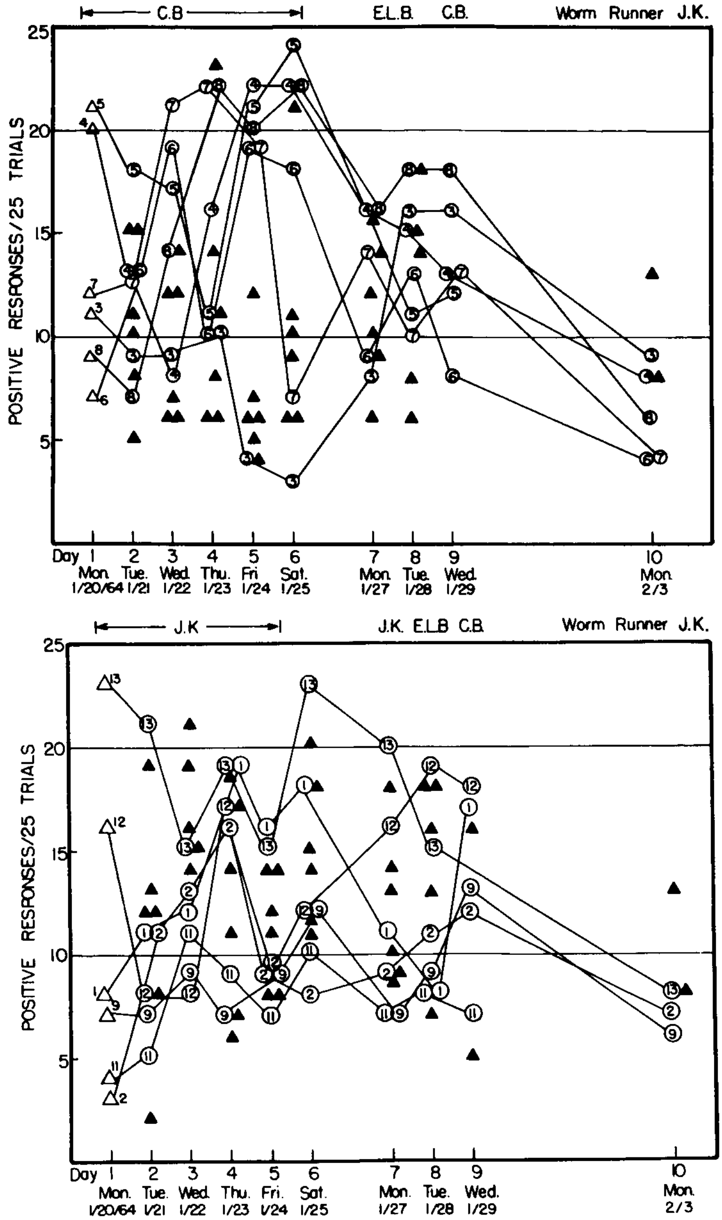


Figure 3. Positive responses/25 trials of D. dorotocephala receiving "tail" shock. The results obtained by one trainer with experimental subjects are indicated by △ , and the results with naive subjects are indicated by ▲ . The results of the other experimenter are indicated by ⊙ (experimental) and ● (naive).



Figures 4A and 4B. Scores of individual D. dorotocephala (numbered circles) tested in LCB-2 using cathode (tail) shock. The isolated triangles represent the scores of naive subjects. The experimenter is indicated at the top of each figure.

In another experiment, D. tigrina were given cathodal shock on either a daily or twice weekly schedule. Each experimenter had at least two naive worms to test daily, in addition to the 10 experimental planarians. No lasting increase in the response rate was noted* in 12 days of daily testing (Fig. 5) or in five training sessions on a twice weekly schedule (Fig. 6). Experimental planarians could not be distinguished from naive.* The results of other experiments using polarized shock were even less indicative of training.

II. Light Habituation

Westerman[10] reported work with D. dorotocephala subjected to a photic stimulus consisting of 25 three-second flashes with a 30 to 60-second intertrial interval. From the initial 26% mean response rate the animals showed a decrease to the set criterion of two successive days (50 trials) with zero responses. The mean number of trials to criterion was 386. Habituation was faster in regenerated offspring of previously habituated planarians, and was also transferred by cannibalism. Thus, this learning resembled light-shock conditioning.

In our laboratories, nine light habituation experiments with 70 D. dorotocephala (Turtox Biological Supply, Chicago) under a variety of conditions of group pretraining or individual training yielded no evidence of habituation. A response was defined as any noticeable deviation in locomotion when a 3-second light burst from two 40-watt lamps was administered. In one experiment, 10 planarians were subjected to 25 trials per day for as many as 25 days. Although four of these planarians did reach a criterion of 50 consecutive trials without a response, on subsequent days of testing these same planarians responded. The mean number of responses did not decrease from the initial 16%; in fact, on two-thirds of the subsequent testing days, the response rate was above 16%. In another experiment, the response rate of 27 planarians previously subjected to 367 pretraining light flashes was 14%; the response rate of 25 planarians with no pretraining was 18%. Thus, a marked difference was not evident in their behavior to the light flashes.

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* Editor's Underline

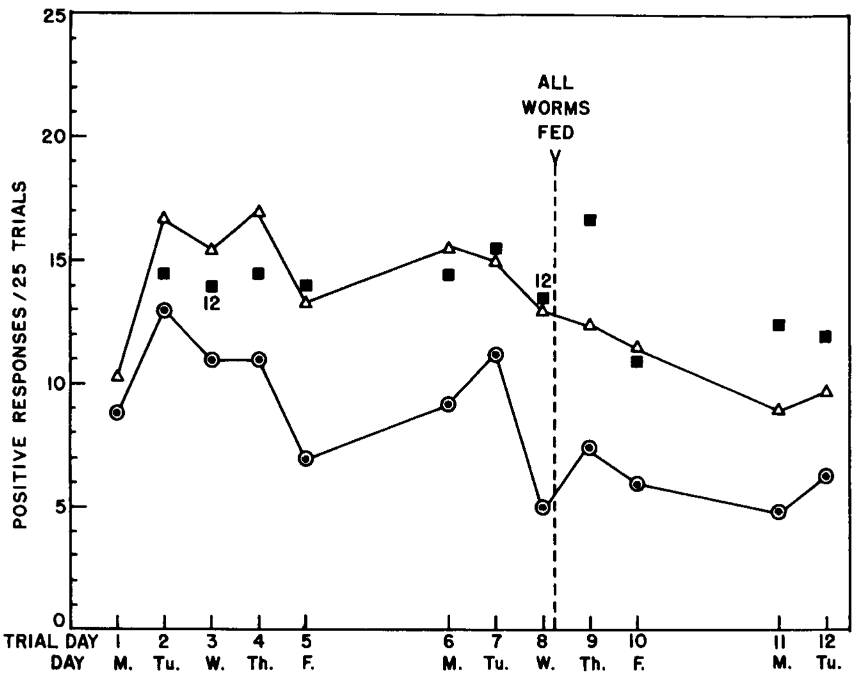


Figure 5. Responses/25 trials of 8 D. tigrina trained daily with cathodal shock as the UCS. Each "worm trainer" trained 4 planarians daily and the average scores are indicated separately by △ and ⊙ . The isolated squares present the results of 4 naive planarians tested each day (12 on trial days 3 and 8). The average score obtained for all naive planarians was 13 by one experimenter and 14 by the other.

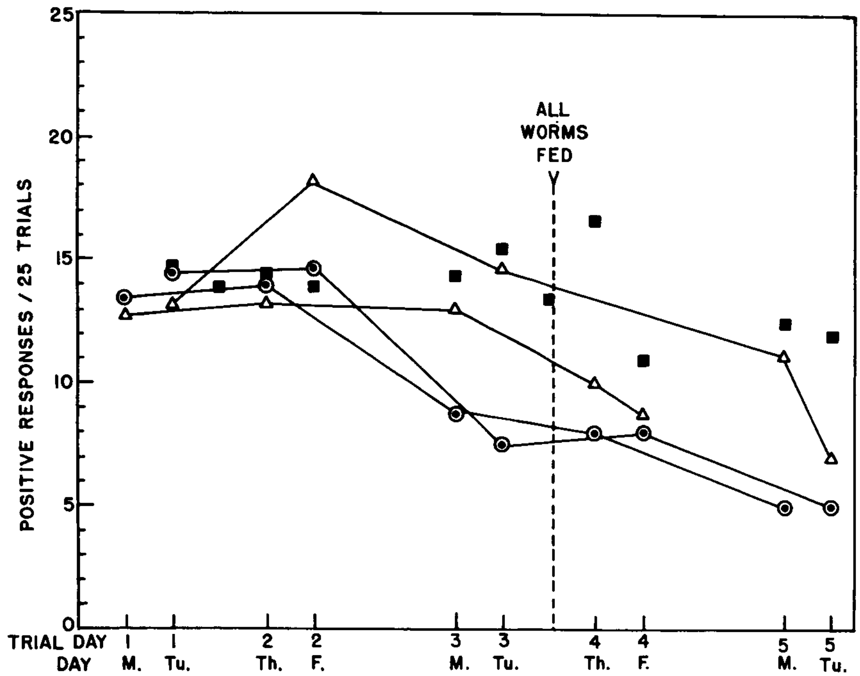
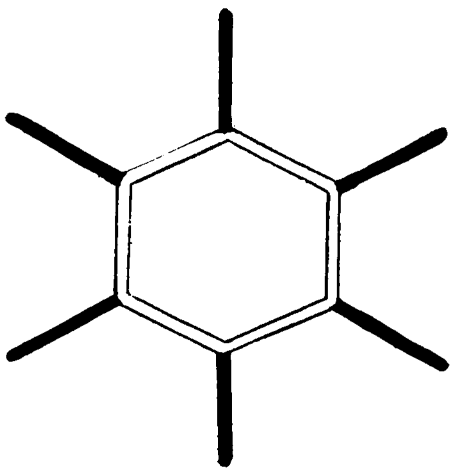


Figure 6. Responses/25 trials for 24 planarians (4 groups of 6) receiving cathodal shock as the UCS twice weekly. One group was tested on a Monday-Thursday schedule, the other group was tested on a Tuesday-Friday schedule. These planarians were tested the same time as those for whom data are presented in Figure 5. Naive planarians were common to both groups.

In a more recent experiment, 12 D. dorotocephala collected locally and with a high naive response to light were subjected to flashing light (3-second flashes at five minute intervals for 20 hours per day) for 10 days. The average response for 25 trials for these planarians was 44%; the response from six subjects maintained for a similar time in "lab-light" was 34%, and the response from planarians kept in a dark cabinet was 68%. The worms from each group were individually coded when tested. This result confirms that some light habituation had occurred, but habituation obtained from "lab-light" was at least as great as that obtained by exposure to approximately 2400 light flashes. The response was clearly not down to the "zero" level reported by Westerman.

III. Maze Training

Various forms of maze training of planarians have been tried. Humphries and McConnell[11] have described in considerable detail a study using a maze consisting of a white hexagon with six black arms, as sketched below:



[Reproduced from The Worm Runner's Digest, V, No. 2, p. 24 (1963).]

This arrangement produced Y-shaped intersections, at each of which the animal was offered a color choice. The correct response consists of circling in the inner white groove; the incorrect response, punished by anodal shock, is scored when the planarian enters a black arm. The optimal conditions are exemplified by Experiments I and J of the report by McConnell and Humphries, from which they conclude that the best training schedule appears to be no more than 30 trials per day, no more than two days of training per week, spaced as far apart as possible, and the use of anodal shock of an intermediate level neither so high as to cause excessive damage to the planarian or so weak that the subject adapts to it readily. The animals should be fed after each set of trials so that they will be maximally hungry by the time the next set of trials occurs, three or four days later. No data have been published on the retention or transfer of this type of maze-learning.

Our maze was very similar to that described except the electrodes were three mm in diameter compared to 1.4 mm. Our maze was wired so that current flowed only between the appropriate adjacent two arms rather than all six. We found that four volts for 1/2 to one second was sufficient shock to cause a definite response from the planarians, whereas Humphries and McConnell used 35 volts for 1.5 to two seconds.

We tested one group of nine <u>D. tigrina</u> on a Monday and Thursday schedule, another group on a Tuesday and Friday schedule for 2 weeks. In each training session 6 previously untested naive subjects were also tested. New code numbers were assigned daily. The individual results are summarized in Table 3. For the 18 experimental planarians, the average percentage of white (correct) choices on successive training sessions was 26%, 45%, 41%, and 36%. In pretraining trails, without shock, these worms had randomly chosen white 43% of the time. For the naive Planarians, the average white choice rate was 30%, 36%, 42%, and 40%. <u>No evidence of general learning was noted and the percentage of correct choices of individual planarians varied greatly from day to day and from planarian to planarian</u>.*

* Editor's Underline

Table 3: Maze-Training of Planarians; Number of White Choices/30 Trials by Individual Planarians in Hexagonal Maze.

Experimenter	Planarian No.	Training Session and Day Run 1 Mon	2 Thurs	3 Mon	4 Thurs	Individual Average for 4 Training Sessions
	1	13	21	18	14	16.5
	2	5	19	23	10	14.2
	3	4	14	8	14	10.0
K	4	24	17	13	11	16.2
	Naive	7,10, 7	15,6, 3	11,4, 10	8,7, 23	
	5	8	11	11	--	8.0
	6	8	10	15	12	11.2
	7	6	4	7	19	9.0
A	8	2	13	11	7	8.2
	9	4	17	6	15	10.5
	Naive	8, 7, 12	11,8, 6	20,19, 8	14,11 24	
		Tues	Fri	Tues	Fri	
	10	7	20	23	13	15.8
	11	14	Not run	13	12	13.0
K	12	6	19	14	2	10.2
	13	13	14	11	7	11.2
	Naive	8, 8, 10	14,13, 5	11,12, 10	9,3, 8	
	14	4	6	Not run	4	4.7
	15	10	10	8	20	12.0
	16	4	19	8	8	9.8
A	17	3	8	17	5	8.2
	18	6	12	3	9	7.5
	Naive	9, 4, 17	9,22, 19	21,14	--	
Average % white choices for each Training Session	Experimental	26	45	41	36	
	Naive	30	36	42	40	

IV. Operant Conditioning

Operant conditioning of planarians to an aversive stimulus has been described by several investigators including Lee[12] and Best.[13] In Lee's experiment, the stimulus was an intense light and the response was the planarian's passage through a narrow light beam directed at an overhead photoelectric cell. The reinforcement was the termination of the intense light for 15 minutes. Responses were recorded and reinforced automatically. A matched control was placed in an adjacent chamber under similar conditions. When the control went under the photocell, the response was recorded, but the light did not go off. Lee reported that the number of half-hour intervals during which one or more responses were made averaged 41% for the experimental planarians and 12% for the controls. Conditioning within 15 hours was noted and response continued at a high rate for 60 hours.

We constructed a very similar apparatus with 4 paired units. Ten minute reinforcement was used. We maintained cell temperature by circulating water from a thermostat-controlled bath and by air cooling. Water was added daily and changed every three to four days. Although there are a number of ways in which data can be expressed, we have chosen for this presentation to express our results in a form roughly comparable to that used by Lee, i.e., the percentage of one-half hour intervals in which a response was made during each period (normally 24 hours) and during the entire experiment. In addition, we noted the number of days in which the response of the matched controls exceeded the experimental subject and vice-versa.

Our experiments with D. dorotocephala and D. tigrina ranged in duration from seven to 21 days, each with four experimental subjects and four controls. We were unable to find any consistent patterns of behavior which would indicate conditioning.* The over-all average of "Percentage of One-Half Hour Intervals" in which the experimental subjects responded was 8.9%; the control average was 10.1%. The highest average for any individual experimental subject was 19% and the maximum individual average for the controls was the same. In a total of 211 worm-days of testing, the

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* Editor's Underline

experimental subjects gave a greater number of positive responses than the controls during 80 worm-days, while the controls gave a greater number of positive responses than the experimentals during 107 worm-days. During 24 worm-days, an equal number of responses were obtained.

In addition, detailed examination of individual patterns of behavior did not lead to the impression that operant conditioning had been achieved. An experimental planarian would, at times, give frequent and consistent responses to light but at other times the same planarian would give few responses for several days, while his control was giving frequent responses.

V. Food Reward

All of the "instructional" procedures described so far use punishment as the reinforcing stimulus. We thought that a reward in the form of food might be a more natural and satisfactory stimulus for planarians. Indeed, one of the earliest reports of training planarians, that of Van Oye[14], states that "planarians could be trained to an unusual route to get food (on a wire below the surface of the water) and the memory of this training survived several weeks of inactivity."

Our experimental design was as follows: *D. dorotocephala* (Dahl Laboratories, Emeryville, Calif.) were maintained singly in 400 ml Pyrex beakers filled to a depth of seven centimeters with "artificial spring water".[15] The reward was small pieces of pork liver held on a small loop of copper wire. The food was initially presented to the experimental group on the center of the water surface. In Experiment I, after 10 days of such presentation, the food was lowered progressively below the surface; then, after the experimental subjects had been allowed to search for food for 45 minutes, the food was removed. In Experiment II, the subjects were allowed to search for food on the top center surface until they found it. The food was presented to the controls in the center of the beaker, but 3.5 cm below the water surface. Planarians are not free swimmers; therefore, in order to get food below the surface, a planarian had to swim to the center and then crawl down the wire. The time required for the planarians to get food was recorded. In each experiment, planarians that had not reached food during testing were

Table 4: Food Reward Experiment I; Minutes Required to Find Food* in Center of Beaker, On and Below Water Surface.

Trial Day	Days After Start	Experimental Subjects** (Minutes)						Control Subjects** (Minutes)					
		#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12
		Food on water surface						Food always 3.5 cm below water surface					
1	0	x	x	x	4	x	9	x	x	x	45	x	x
2	2	x	x	x	17	x	35	x	x	x	x	x	x
3	5	x	34	x	35		x		x		24		40
4	7		15	23	x	17	27						
5	9	x	x	15	x	x	x	x	x	x	x	x	x
6	12	30	x	42		15							
7	14	x		x		x	14		23				
8	16	35	10	x	7	x	3	x	x	x	x	x	x
9	19		25	30		35							
		Food 0.5 cm below											
10	21			33		25	3		23				
11	23		35	10									25
12	26		40	44			30						
		Food 1.0 cm below											
13	28	35	36		42			11					30
14	30	25	5	x	x	x	x	x	x	x	x	x	x
15	33			25		15							
16	36	8		20									
17	38												
		Food 2.0 cm below											
18	42	35	30			42							
19	48		40										
20	52	x	x	x	x	x	x	x	x	x	x	x	x
21	55		40	45				20		10			
22	57		30										

* An x in a square indicates that after 45 min. of unsuccessful searching for food, the planarian was presented with food in an "easy" position in the bottom of the beaker. The other planarians on that trial day did not eat.

** When the food was presented to the experimental planarians in the center of the beaker on the water surface for 45 min., the subjects found food in 35% of the 54 opportunities; when presented food 0.5 cm below the surface, the subjects found food in 44% of 18 opportunities. The subjects found food 1.0 cm below the surface in 30% of 30 opportunities, and food 2.0 cm below the surface was found in 23% of 30 opportunities. The control subjects found food in 5% of the trials.

Table 5
Food Reward Experiment II
Minutes Required to Find Food

Trial Day	Days After Start	Experimental Subjects*						Average Time	Control Subjects** Position A						Control Subjects** Position B					
		#1	#2	#3	#4	#5	#6		#7	#8	#9	#10	#11	#12	#7	#8	#9	#10	#11	#12
1	0	5	15	40	--	50	--	--	--	--	--	15	--	--	Not done					
2	2	10	10	35	10	25	50	23	15	--	--	--	--	10	Not done					
3	5	14	10	7	30	32	18	18	--	--	--	--	--	--	24	20	8	5	11	9
4	7	50	3	40	6	32	40	28	--	--	--	15	--	--	Not done					
5	10	68	34	105	21	81	145	76	--	--	--	--	--	--	1	1	65	1	--	--
6	16	22	315	7	58	73	62	40	--	--	--	--	--	--	8	20	13	10	11	40
7	22	30	90	58	68	40	40	46	--	--	45	--	--	--	38	--	20	7	21	3

* The experimental subjects were presented with liver suspended on a wire in the center of the beaker on the water surface for 3 hours per session.

** The control subjects were presented with liver suspended at middle of beaker, 3.5 cm below the water surface for one hour (Position A). On 4 days, the liver was lowered to the bottom of the beaker for 2 additional hours (Position B).

given food on the bottom of the beaker at weekly or biweekly intervals as indicated in Tables 4 and 5.

From the results we have made the following conclusions: (1) There is no evidence in the simplest case, with food suspended in the center of the water surface of a 400 ml beaker, that planarians found food either faster or with a higher frequency as the number of trials increased (with the possible exception of subject No. 2, Experiment I). The average time required to find food presented in this manner did not decrease over seven to nine training sessions spaced over a three week interval. Individual planarians did not show a consistent ability to find food. (2) When the food was submerged below the surface, the planarians required longer to find it, and found the food with decreasing frequency as the depth increased. (3) Control planarians found food presented below the surface in 5% of the trials in Experiment I and 9% of the trials in Experiment II. (4) The results of Experiment II indicate that planarians presented with food in an "easy" situation on the bottom of the beaker found it quickly and reliably. This reduces the likelihood that the results were obtained solely because the planarians were either not hungry or did not like pork liver.

SUMMARY

Unsuccessful efforts to demonstrate learning in planarians by classical conditioning, light habituation, maze-learning, operant conditioning, and food reward methods are described. Until more adequate and more useful methods and descriptions of methods to train planarians are available, this animal appears to have little utility for proposed studies of the possible biochemical bases of learning.

ACKNOWLEDGEMENTS

This work was sponsored in part by the United States Atomic Energy Commission. The experimenters were various members and associates of the Laboratory of Chemical Bio-dynamics and included Allan Jacobson, Reeva Jacobson Kimble, Jo Anne Keller, Janet Alvarez and Marie Herbert. Dr. C. D. Barnes of the University of California Medical School collaborated in one of the experiments. The frequent and valuable electronic assistance of Mr. Frank Upham is also gratefully acknowledged.

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* * *

MEMORY STORAGE

AND LOW-TEMPERATURE BIOLOGY

A Discussion Paper,
Dated August 19, 1964

by

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LEARNED INFORMATION MIGHT in the limit be stored in two possible ways. Either the information might be stored in structures (whether at a molecular or a cellular level), or the information might be stored in processes (such as regenerating electrical pulses). In principle, it should be possible to distinguish between these two modes of storage, by subjecting the organism storing the memory to conditions which obliterate the processes while retaining structure. The organism must, of course, be able otherwise to survive these conditions.

Consider for a moment the distinction between structure and process in statistical mechanics for a limitingly simple case. An atom may be described by three position coordinates and three momentum coordinates. At any time structural information is largely related to the position coordinates, while process information is related to the momentum coordinates. If we reduce the temperature of the system to near absolute zero, then all momentum values fall to zero (disregarding for the moment zero-point vibration). If all momentum coordinates are zero, then there can be no information stored in process as outlined above.

Clues from Cryobiology

It has been known for many years that a number of living systems may be subjected to temperatures near absolute zero and then returned to their normal temperatures with no loss of biological function; that is, the systems survive temperatures very near to absolute zero.*

A very significant conclusion from these experiments is that the information necessary to specify a living system is structural. Put in a somewhat more dramatic way, if we wished in principle to synthesize a living organism, we need only to synthesize the appropriate structure; we do not need to produce an energy or momentum distribution. The appropriate processes will follow entirely from the structure when the structure is placed in the right environment. That this is true for both genetic and morphogenetic information is shown by the fact that Artemia eggs, maintained within two degrees of absolute zero for a week, when rewarmed and placed in salt water, went through a normal hatching process (Skoultchi and Morowitz, 1964, in press, Yale J. of Biol. & Med.).

The question then arises: Will learned information persist if the organism is taken to temperatures near absolute zero? To pose this question experimentally requires an animal that will both learn and survive temperatures near absolute zero. Low-temperature survival has been reported** in adult organisms of three groups of animals, namely: (arranged in ascending phylogenetic order) rotifers, nematodes, and tardigrades.***

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*EDITOR'S NOTE: For reviews of these experiments see the works cited at the end of this discussion paper in the list of "Further Recommended Reading," particularly B. J. Luyet and P. M. Gehenio, Life and Death at Low Temperatures (Biodynamica, Normandy, Missouri, 1940).

**Luyet and Gehenio, ibid.

***EDITOR'S NOTE: In this connection it seems relevant to cite a paragraph from the article "Tardigrada" by R. W. Pennak, in The Encyclopedia of the Biological Sciences, ed. by P. Gray (Reinhold, New York, 1961):

"One of the most remarkable features of tardigrade biology is the ability of many [footnote continued on facing page]

No reports are known to us of learning experiments in any of these three groups. However, recently reported learning experiments using flatworms (planaria) suggest the possibility of learning in organisms both phylogenetically lower and neurophysiologically less complicated than those here discussed.*

Of the three groups of animals under consideration, rotifers and nematodes appear to have somewhat simpler nervous systems than tardigrades; the first consisting of a large cerebral ganglion and smaller ganglia associated with the mastax and foot, with numerous other nerves leading to muscle and sense organs. Nematodes also possess numerous ganglia, nerves, and neuromuscular connections. Tardigrades, probably having the most highly developed nervous system and sensory apparatus, appear therefore to be most suitable for learning experiments.

Tardigrade Nervous System

The following neuroanatomical description is taken from the Cambridge Natural History; for a diagram of the tardigrade nervous system, see Fig. 1.

"The nervous system consists of a brain or supra-oesophageal ganglion, whose structure was first elucidated by Plate, and a ventral chain of four ganglia. Anteriorly the brain is rounded, and gives off a nerve to the skin; posteriorly each half divides into two lobes, an inner and an outer. The latter bears the eye-spot when this is present. Just below this eye a slender nerve passes straight to the first ventral ganglion. The brain is continued round the oral cavity as a thick nerve-ring, the ventral part of which forms

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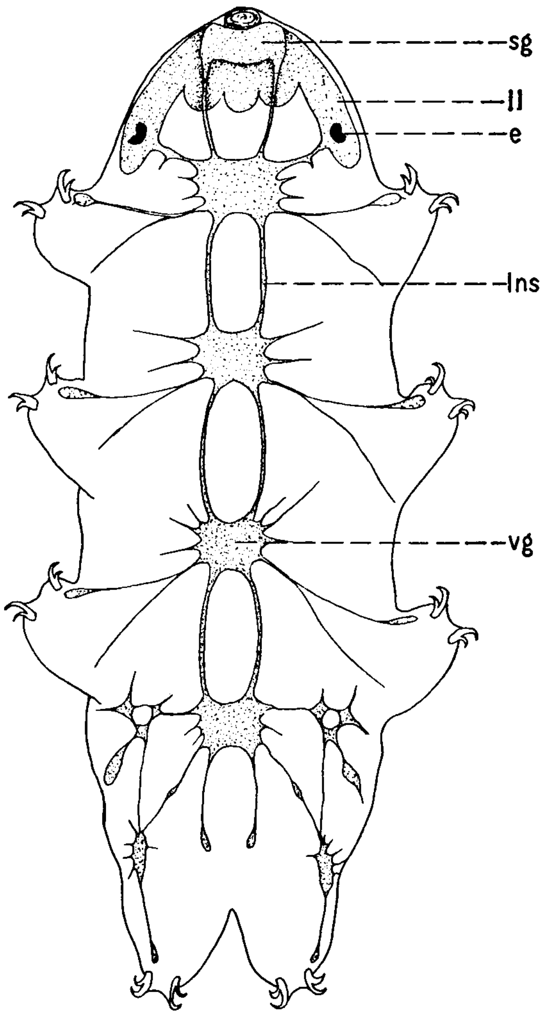
[footnote continued from previous page] species to survive dessication. When the habitat dries up, the tardigrade contracts and shrivels into a wrinkled spherical mass which may persist in a state of suspended animation for many years, in spite of exceptionally high or low temperatures and an absence of water. When ecological conditions again are suitable, the animal becomes turgid and resumes its normal activities in a few minutes to a few hours."

*The author recently learned of the article by Bennett and Calvin, published in this issue of the NRP Bulletin. The possibility of learning in the organisms discussed here should therefore be considered independent of flatworms. --H.J.M.

Figure 1. VENTRAL VIEW OF TARDIGRADE NERVOUS SYSTEM



Tardigrades are fresh-water invertebrates usually less than 500 microns in length. Shown here is a ventral view of the nervous system of Macrobiotus, X220. e, eyespot; ll, lateral lobe of brain; lns, longitudinal nerve strand; sg, subpharyngeal ganglion; vg, ventral ganglion. (Modified from various sources.) [Reproduced from Pennak, R. W.: Fresh Water Invertebrates of the United States (Ronald Press, New York, 1953, p. 246)].

the sub-oesophageal ganglion, united by two longitudinal commisures to the first ventral ganglion. Thus the brain has two channels of communication between it and the ventral nerve-cord on each side, one by means of the slender nerve above mentioned, and one through the sub-oesophageal ganglion. The ventral chain is composed of four ganglia connected together by widely divaricated commisures. Each ganglion gives off three pairs of nerves, two to the ventral musculature, and one to the dorsal. The terminations of these nerves in the muscles are very clearly seen in these transparent little creatures though there is still much dispute as to their exact nature."

Summary

What is here being proposed is that experiments be undertaken to investigate learning in tardigrades, nematodes, and rotifers. Tardigrades are probably the first choice, followed by nematodes and then rotifers. The learned animals could then be taken to temperatures near absolute zero. Following this treatment the retention of learned information could be tested. If the information were retained, it would be unambiguously established that learned information can be stored in structure. Thus, it should in principle be possi- to distinguish between the storage of learned information in structure or in process.

RECOMMENDED FURTHER READING

On Cryogenics in General*

A good short summary of low-temperature physics will be found in Harrie Massey's The New Age in Physics, Chapter 3 (Harper, New York, 1960).

For more detail on cryogenic processing, see "Extremely Low Temperatures ... Production and Commercial Uses" in Chemical Engineering, Feb. 23, 1959. A good book that enlarges on this subject is Cryogenic Engineering by R. B. Scott (Van Nostrand, Princeton, N.J., 1959).

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*EDITOR'S NOTE: Adapted from International Science and Technology.

A recent introductory account of the uses of low temperatures is provided in Michael McClintock's Cryogenics (Reinhold, New York; Chapman and Hall, London, 1964).

Continuing developments in the field can be followed through Advances in Cryogenic Engineering, the proceedings of a series of symposia held in different U.S. locations (Plenum Press, New York, Vols. 1-6).

On Cryozoology*

Work prior to 1940 is summarized succinctly in the classic book by B. J. Luyet and P. M. Gehenio, Life and Death at Low Temperatures (Biodynamica, Normandy, Missouri, 1940), now out of print, but available in most libraries.

One book-length treatment, namely Audrey Smith's comprehensive Biological Effects of Freezing and Supercooling, contains a fascinating chapter, "The Revival of Mammals from Body Temperatures Below Zero," that describes work carried out by Dr. Smith and her colleagues in Great Britain (Williams & Wilkens, 1961, published in England by Edward Arnold, Ltd.).

Read Cryogenic Technology, edited by Vance (Wiley, 1963), for Rinfert's Chap. 16 entitled "Cryobiology."

Several excellent symposia devoted to cryobiology have been held; see Recent Research in Freezing and Drying, edited by Parkes and Smith (Thomas, 1960, published in Great Britain by Blackwell); then, for a summary of other recent research in cryobiology, "Freezing and Drying of Biological Materials" in Annals of the New York Academy of Sciences, 85, 501 (1960).

Finally, read the article "Cryobiology" by G. F. Doebbler and C. W. Cobbley, in International Science and Technology, June 1964, pp. 58-71.

On Tardigrades and Their Nervous System

The tardigrades have not been thoroughly studied. The most recent review is by G. Ramazzotti, a monograph called Il Phylum Tardigrade (Volume 14, Memorie Istituto Italiana di Idrobiologia, 1962). An older German review may be found in

*EDITOR'S NOTE: Adapted from International Science and Technology.

E. Marcus' Klassen des Tierreichs, Band 5, Arthropoda, Abt. 4, Buch 3; pp 1-608 (Akademische Verlangsgesellschaft, Leipzig, 1929).

Our description of the tardigrade nervous system was taken from the Cambridge Natural History, Vol. IV, ed. by S. F. Harmer and A. E. Shipley (Macmillan and Co., Ltd., London, 1909).

The source of our illustration, which also contains a section on tardigrades, is R. W. Pennak's Fresh Water Invertebrates of the United States (Ronald Press, New York, 1953).

On Rotifers and Nematodes

The last named book cited above covers these animals.

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THE EIGHTH STATED MEETING OF NRP ASSOCIATES

MONDAY, AUGUST 10

Morning

* NRP Chairman Francis O. Schmitt opened the meeting by introducing a number of distinguished guests: Dr. Edgar A. Bering, Jr.; Dr. Carl R. Brewer; Professor Paul Glees; Dr. Bronislav Janković; Dr. Lawrence Levine; Dr. Ljubodrag Mihailović; Professor George A. Miller; Dr. Robert Morison; Mr. Israel Rogosin; Dr. Betty Geren Uzman; and Dr. Rudolf von Baumgarten.

* Chairman Schmitt then introduced Associate Robert Galambos, Chairman of the NRP Work Session on Glia, held on June 2-3, 1964. Professor Galambos presented an interpretive summary of that symposium. It will be reported in a forthcoming NRP Bulletin.

Afternoon

* Associate Walle J. Nauta introduced Professor Paul Glees of Göttingen. Professor Glees first spoke on ribosomes and the endoplasmic reticulum in relationship to the maturation of neurons and synapses, then showed a film on the behavioral effects of small lesions in the hand area of monkey sensory cortex.

* Associate Albert L. Lehninger introduced Associate Melvin Calvin, who gave an oral summary of the mainly unsuccessful attempts of his laboratory to train planarians as described in the literature. These 12 man-years of attempts are reported in a discussion paper elsewhere in this issue.

Evening

* Executive Session.

TUESDAY, AUGUST 11

Morning

* Chairman Schmitt introduced Associates Manfred Eigen and Leo DeMaeyer, Chairmen of the NRP Work Sessions on Storage, Transfer, and Fast Readout of Information in Macromolecules held on May 7-8 and August 7, 1964. Dr. Eigen then gave an interpretive summary of these symposia, the first of which has already been partly reported in the May-June, 1964 NRP Bulletin; Dr. Eigen's final evaluation will appear in a forthcoming issue of the Bulletin, supplemented by contributions from some of its participants.

Afternoon

* Chairman Schmitt introduced Professor Lawrence Levine of Brandeis, who was Chairman of the NRP Work Session on Immuno-Neurology held on July 23-24, 1964. Professor Levine gave an evaluative summary of that symposium, augmented by presentations made by two of its participants -- Dr. Peter F. Davison of MIT, who spoke on the work of Dr. Huneeus-Cox on Axonal Proteins as Antigens, and Professor Ljubodrag Mihailović of Belgrade, who spoke on his work with Professor Janković on Brain Regions as Antigens. These reports will appear in a forthcoming issue of the NRP Bulletin.

WEDNESDAY, AUGUST 12

Morning

* Associate Robert B. Livingston introduced Professor George A. Miller of the Harvard Center for Cognitive Studies. Professor Miller gave an account of the history of this 5-year-old organization, which studies Perception, Cognitive Development, Symbolic Processes, and Memory, and of the fascinating current work in each of those fields.

Afternoon

* Associates Melvin Calvin and Albert L. Lehninger were Chairmen of a session that heard progress reports on the research of a number of NRP Associates as part of a discussion of NRP-related investigations at Associates' laboratories.

Without making a systematic survey of every research project at every Associate's laboratory that has been inspired or affected by the NRP,* it is still easily possible to list the following current investigations that are attempting to advance scientific understanding of the physical basis of human mental functions, from the behavioral to submolecular levels:

Psycho-biological neuro-anatomy	Walle J. H. Nauta
Electrophysiological studies of the brain	Robert Galambos
Parameters of impulse trains; recognition units in nervous systems	Theodore H. Bullock
Nerve protein studies	Francis O. Schmitt
Optical studies of nerve under excitation; protein conformation changes	Michael Kasha
Electron microscope and bio-chemical studies of multi-enzyme complexes	H. Fernandez-Moran
Stereo-specific allosterism	Albert L. Lehninger
RNA replication	Severo Ochoa
Neuronal and glial RNA base-ratio changes	Holger Hydén
Molecular organization and mental function	Leroy G. Augenstein

* Associates cooperate through the NRP in more than laboratory researches and semi-annual Stated Meetings. They also serve as Work Session planners, chairmen, participants, and critics; and, as the "faculty" of this multidisciplinary "invisible college," they will comprise the core of the teachers at future intensive study programs in the neurosciences.--T.M.

Conformation changes in polypeptides and polynucleotides; enzyme action; very rapid chemical transformations; effects of high electrical fields on chemical equilibria and on cooperative processes	Manfred Eigen and Leo DeMaeyer

It was agreed that, as a result of NRP meetings, new projects were underway that might not otherwise have occurred as readily or at all. For example, Professor Lehninger pointed out that, through personal interactions started at the NRP Center, he had begun trans-Atlantic and trans-Mediterranean collaborations with Manfred Eigen of Göttingen and Aharon Katchalsky of Rehovoth. Also mentioned was the impetus given the new science of immuno-neurology by the exchanges of techniques and materials between Belgrade, New Haven, and Montreal, arranged at the NRP Work Session on Immuno-Neurology. --T.M.

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N E W S   A N D   V I E W S

On Meetings and Organizations

Oct. 5-6	Enzyme Regulation (3rd international symposium), Indianapolis, Indiana (G. Weber, Indiana U. School of Medicine, Indianapolis, Indiana)
Oct. 13-17	Electron Microscopy Society of America (22nd annual), Detroit, Michigan (A.R. Taylor, Virus Div., Parke Davis & Co., Detroit 32, Michigan)
Oct. 15-16	Bioenergetics Symposium, U. of Western Ontario, London, Ontario, Canada (K.P. Strickland, Dept. of Biochemistry, Faculty of Medicine, U. of Western Ontario, London, Ontario, Canada)
Oct. 15-17	Central Neuropsychiatric Association, Denver, Colorado (W.P. Shelton, 8215 Westchester Drive, Dallas 25, Texas)
Oct. 17-18	Society for Psychophysiological Research (4th annual), Washington, D. C. (L.A. Gustafson, SPR, 74 Fenwood Road, Boston, Massachusetts)
Nov. 11-13	American Society for Cell Biology (4th annual), Cleveland, Ohio (Dr. David E. Green, Inst. for Enzyme Research, 1710 University Avenue, Madison 6, Wisconsin) Among those scheduled to deliver papers are D.E. Green, A. Lehninger, H. Fernandez-Moran and B. Chance.
Nov. 11-14	Symposium on Models for the Perception of Speech and Visual Form, Boston, Mass. (A. Cushman, Wentworth Institute, 550 Huntington Ave., Boston, Mass.) Scheduled participants include R. Jakobson, D. M. McKay, O. Selfridge and G. Miller.

Nov. 12-13 Research Conference on Nerve as Tissue, Lankenau Hospital, Philadelphia, Pa. (Kaare Rodahl, Dir. of Research, Lankenau Hospital, Philadelphia, Pa.)

*Nov. 30-Dec. 2 Symposium on Thalamic Regulation of Sensorimotor Activities, Columbia University, New York, New York (Dr. M. D. Yahr, N. Y. Neurological Institute, 710 W. 168th St., New York 32, N.Y.)

About People

BRITTON CHANCE has been named to the newly created position of Eldrige Reeves Johnson Professor of Biophysics in the Department of Biophysics at the University of Pennsylvania School of Medicine.

ARTHUR SILVERSTEIN, formerly at the Armed Forces Institute of Pathology in Washington, D. C., is now an Associate Professor at the Wilmer Institute, Johns Hopkins University School of Medicine, Baltimore, Maryland.

Among those receiving an honorary Doctor of Science degree at the opening ceremonies of the University of Pennsylvania School of Medicine's bicentennial was SEVERO OCHOA. Other recipients, all of whom were honored for furthering knowledge of cell dynamics, were ARTHUR KORNBERG, JOHN ENDERS, WENDELL STANLEY, and GEORGE BEADLE.

A new book on the molecular basis of mitochondrion structure and function was published recently by ALBERT LEHNINGER. Entitled The Mitochondrion, its publisher is W. A. Benjamin, Inc., of New York.

From Publications

The New Scientist (No. 408, 10 Sepember 1964) contains an article by NRP Chairman F. O. Schmitt, "Molecules and Memory", in which he writes:

> "If the synaptic cleft is indeed the arena where 'selfhood' of the neuron is expressed,

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* Noted also in the May-June 1964 Bulletin.

> where its molecular-recognizing proteins play their crucial role in implementing alterations imposed by sensory information, then this site deserves intensive ultrastructural, biochemical and biophysical study."

In an exchange of open letters between VICTOR WEISSKOPF of MIT, and ALVIN M. WEINBERG, Director of the Oak Ridge National Laboratories, appearing in the June 1964 issue of Physics Today, Dr. Weinberg wrote:

> "As a physicist, I am enchanted and astonished by the wonderful new symmetry principles, and their violations, and am convinced that a clearer understanding of where the elementary charge comes from, or the reason the nuclear force saturates, would be intellectual gems that we who are even a little trained in physics could gain enormous satisfaction from. But there are other gems that I personally also would find at least as satisfying: the elucidation of just what protein in the brain is the memory element; or what mechanism governs cellular differentiation; or why the universe expands." (Editor's underline)

The impact of the molecular approach to learning and memory on the field of psychology is beginning to be evident in the psychological literature. Two recent review articles of note are "Neurochemistry and Learning", by John Gaito and Albert Zavala, appearing in Psychological Bulletin, 1964, Vol. 61, No. 1, 45-62; and "Two Hypotheses Concerning the Biochemical Basis of Memory" by Thomas K. Landauer in Psychological Review, May 1964, Vol. 71, No. 3. We quote the abstract of the latter article:

> "The 1st hypothesis is that the basic event of conditioning or learning is the transfer of RNA molecules from surrounding glial cells into conducting neurons and the subsequent transformation of the protein synthesizing apparatus of the neuron. The transfer of RNA across membranes (of activated neurons only)

is presumed to be due to electrophoretic migration in the reversed potential gradient during impulse conduction. The 2nd hypothesis is that information is coded for storage in the CNS in the form of frequency characteristics of spreading ac potentials to which a neural membrane can become tuned by alteration of its protein structure. Together, the 2 hypotheses suggest the basis of a physiological theory of learning."

NRP in the News

Reports on the work of NRP and its Chairman, Francis O. Schmitt, have appeared in several non-scientific publications recently:

In August, the Boston Globe carried a week-long series of feature articles by Herbert Black. Noting the role of NRP in facilitating interdisciplinary communication, Mr. Black concluded:

"Good communications is one of the features that gives the invisible college in Brookline added importance. Stress is being placed on communications so that all scientists studying mind and memory, even those of different fields and backgrounds, can understand what is being learned. The Neurosciences Research Program is taking an advanced position on this."

Modern Medicine, in its August 17 issue, contained a feature article on F. O. Schmitt, as one of its series called "Contemporaries."

The Insider's Newsletter (Cowles Magazines and Broadcasting, Inc.) of September 14 contained a glamorized blurb about the NRP, apparently derived from Mr. Black's articles in the Boston Globe, and definitely not checked with NRP before publication.

On September 19, Communications Director T. Melnechuk gave a talk on "Mind & Molecule" to the Boston Chapter of Mensa.

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